STUDIES IN THE MORPHOLOGY OF *SELAGINELLA PUMILA*, SPRING.

Part I.—The Vegetative Organs of the Sporophyte.

By A. V. Duthie.

(With twenty-six Text-figures.)

With the exception of a doubtful record from Natal, this small annual species of *Selaginella* is known only from the Cape Province. It has been collected in most of the coastal districts from the Cape Peninsula to Alexandria, and has recently been found as far inland as Tulbagh. As the species is inconspicuous and might easily escape the notice of collectors, it is probable that its distribution is more general than is usually supposed. In the Stellenbosch district it occurs abundantly from July to October, and is generally found on clayey soil associated with liverworts and mosses and forming part of the annual flora of flats and hill slopes. It has also been found growing luxuriantly in water-logged turf by the side of trickling water.

So far as I am aware, the only recent work dealing with the species is contained in a paper by Sykes and Stiles (15) which appeared in the Annals of Botany in 1910.

The observations embodied in the present paper have extended over several years, and have brought to light certain interesting features, some of which do not appear to have been recorded for other species. The paper deals chiefly with the external morphology and anatomy of the vegetative organs of the sporophyte. A general discussion of the results will be postponed until after the completion of the work.

Sclechtendal (10) figured two varieties of *S. pumila*, namely, *pygmaeum* and *bryoides*, differing in size, the latter being the larger and more procumbent. Hieronymus (6) recognises two distinct species under the names *S. pumila*, Sclecht., and *S. bryoides* (Kaulf.), Hieron., the former characterised by lanceolate, the latter by ovate, leaves. The characters upon which the two species or varieties have been based are found, on the examination of material from different parts of the Stellenbosch district, to overlap to some extent. Specimens gathered in shaded situations on hill slopes are delicate and often more or less procumbent, with ovate leaves; while those gathered on exposed flats are wiry and erect, with lanceolate leaves. Variations in the leaf form may occur in a single specimen, especially if the environment be altered during growth (fig. 1). Two instances of lobed leaves were noted (fig. 2); but these are obviously to be regarded as abnormalities. Individual plants vary greatly in size. Fruiting specimens of 1 cm. are not uncommon, while the tallest plants noted reached the height of 19 cm. By far the greater number are branched; but small unbranched specimens are occasionally met with.

An excellent figure of the leafy stem and cones of the flats type occurs in Marloth's Flora of South Africa, vol. i, fig. 60. 1.; while the more

Fig. 1.

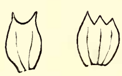


Fig. 2.

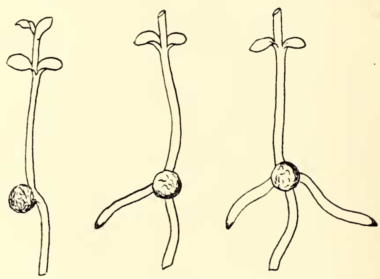
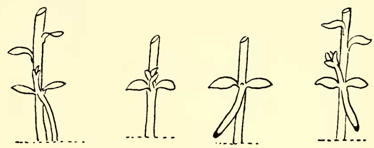


Fig. 3.

delicate hillside type is figured by Sim (14). Neither of these drawings, however, gives a correct impression of the root-system of the plant. As in the majority of described species of *Selaginella* (6), three roots first arise at the base of the hypocotyl in the neighbourhood of the spore, the middle one being the main root of the sporeling (fig. 3). Each of these roots may branch laterally. The erect and slender hypocotyl, which may reach the height of about 4 mm., bears the two oppositely placed cotyledons and the plumule which is later continued into the leafy stem (fig. 4). Additional erect or sub-erect stems with independent root-systems may arise laterally from the upper part of the hypocotyl.* The first of these secondary stems originates midway between the cotyledons either before or after the appearance of its root-supply (fig. 5, *a–d*). A second stem with its root may arise at the same level in the neighbourhood of the first, and this process may be repeated until, in hardy specimens, a tufted habit results (fig. 6,

* It is probable that this apparent lateral shoot should be regarded as a delayed branch of the first stem dichotomy, the erect axis representing the produced branch.

a, *b*). All such secondary axes arise on one side only of the hypocotyl, and their roots grow down through the air for about 2 mm. before striking the soil (fig. 5). Attempts to induce the formation of adventitious roots at other points by means of cuttings or layerings have been unsuccessful. With a little care the secondary stems with their roots can be removed, leaving the primary stem with the cotyledons and trident root-system intact (fig. 7). Both primary and secondary stems may remain unbranched above or produce in one plane a varying number of short lateral branches



d *b* *a* *c*

FIG. 5.

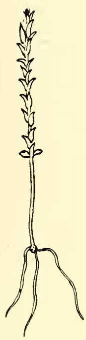
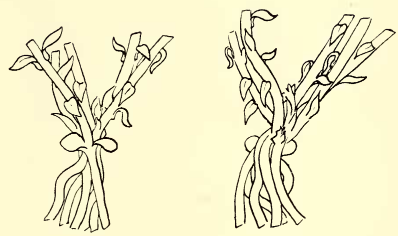


FIG. 4.



a *b*

FIG. 6.

each ending in a cone. One or more of the secondary stems may eventually overtop the main stem. The secondary roots may also branch laterally.

The detailed anatomy of the tissues from which these secondary axes and their roots originate, also the minute structure of the growing points of root and stem, will be dealt with in a later paper.

The symmetry of erect and evenly illuminated shoots is radial. The leaves are all of the same size, and are arranged in four vertical rows along the surfaces of the four-sided stem. Though at first sight the phyllotaxy appears to be somewhat irregular, it is found on examination to be a modification of the usual decussate arrangement. The two leaves belonging to each pair do not arise at exactly the same level, and later may become more or less widely separated as the result of the elongation of the intervening stem tissue (fig. 8). This difference in level may sometimes be observed in the cotyledons themselves. Fig. 9 shows the cotyledons and the succeeding leaf pair cleared in caustic potash. It will be noticed that not only do the leaves of each pair differ in size, but also that the leaf-traces of the two cotyledons are inserted on the stele of the axis at slightly different levels. Decussate leaves are often present at the base of the plant, and may appear at other points as well. In the specimen, a part of which is illustrated in fig. 10, the two opposite cotyledons were followed by four evenly spaced leaves. After these came five approximately decussate leaf pairs, then one whorl of three leaves, and finally eight leaves evenly spaced. Tall-

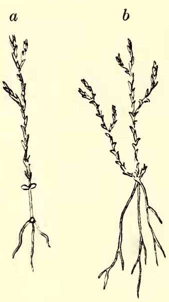


Fig. 7.

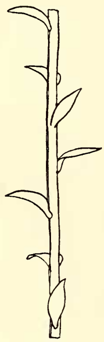


Fig. 8.

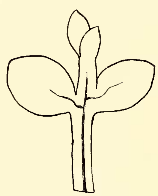


Fig. 9.

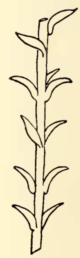


Fig. 10.

stemmed plants growing in shaded situations often show a considerable interval between the two leaves of a "pair," combined with a certain amount of stem torsion which serves to obscure the phyllotaxy.

While specimens from the flats are usually wiry and erect-stemmed and show typical radial symmetry, the dorsiventral condition is occasionally approximated to, especially in hardy plants where several basal stems form a close, erect tuft. On such stems the leaves appear to be shifted slightly so as to face towards the periphery of the fascicle (fig. 11). Small plants collected in 1918 on sloping ground which had been ploughed over some time before and from which all larger plant growth was absent, showed for the most part erect stems with radial symmetry. Specimens were, however, found in shaded hollows of the uneven soil which exhibited prostrate secondary axes and a marked dorsiventrality. In one of these specimens the leaves on the shaded side were distinctly larger than those on the illuminated side of the stem (figs. 12, 13). This transition from the isophyllous to the anisophyllous condition does not appear to have been observed before in this species.

The root of *S. pumila* is entirely devoid of root hairs. The mycelium of an endophytic fungus was found to be present in all the material examined,

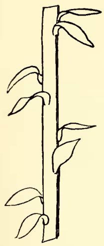


Fig. 11.

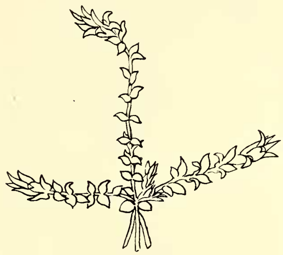


Fig. 12.

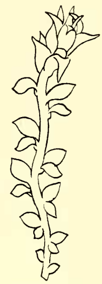


Fig. 13.

and is especially abundant in the large cells of the inner cortex (figs. 14, 15). It is probable that infection of the root cells takes place through the epidermis, as hyphae are often observed in contact with the outer surface of the root and occasionally in the cavities of the epidermal cells. The hyphae appear to be restricted to the subterranean parts of the root system.

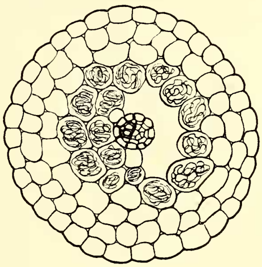


Fig. 14.

The nature of the fungus, its mode of entry into the root and the relationship existing between the two plants, will be dealt with in a later paper. Bruchmann has recorded the presence of an endophytic fungus together with the absence of root hairs for *S. spinulosa* (1) and *S. preissiana* (3), while Janse (6) has reported fungus mycelium in the roots of certain Javanese species of the genus. More recently Uphof (16) has described and figured traces of fungus mycelium in *S. rubella*.

The epidermal cells of the root are somewhat papillate and, as age advances, the outer walls may become markedly thickened. This thicken-

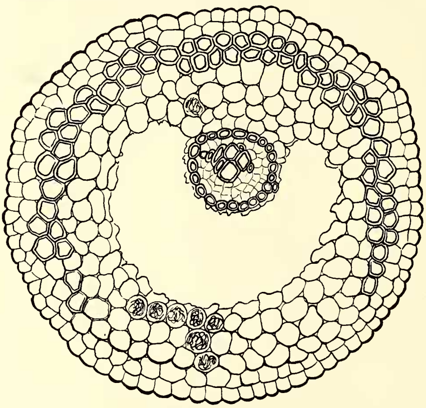


Fig. 15.

ing of the walls may extend to the outer cortex, or (fig. 15) the epidermis and cell layer immediately next to it may remain comparatively thin while a zone of the middle cortex is strongly thickened. Chlorophyll is present

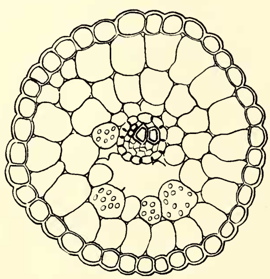


Fig. 16.

in the cortex of the aerial region of the young root (fig. 16). It is worthy of note that in all essential features this aerial part of the root is similar in structure to the subterranean part.

An interesting feature of the root of *S. pumila* which does not appear to have been recorded for any other species of the genus is the presence of a well-marked air cavity in the inner cortex lying on the phloem side of the stele (figs. 14, 15, 16). This intercellular space arises by the separation and breaking down of some of the inner cortical cells, the remains of which may often be seen still adhering to the endodermis. The resemblance of a transverse section through an old root of *S. pumila*, with its enlarged air cavity and eccentric stele, to that of *Isoetes* (12) or *Stigmaria* (11) is very striking (fig. 15). The resemblance to the latter was found to be still more marked in hardy, tufted plants preserved in formalin alcohol. Here the cavity in the basal region of old roots appeared to have extended right round the endodermis, isolating the central stele completely.

The endodermis of the root is well defined. The cells when young show the usual radial cuticularisation (figs. 14, 16), but later the entire walls

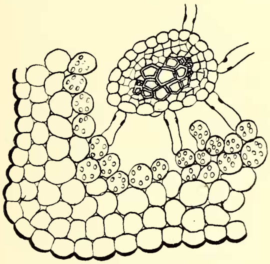


FIG. 17.

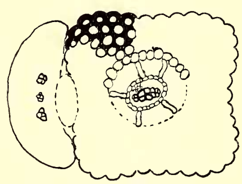


FIG. 18.

become strongly thickened (fig. 15). As in other investigated species of *Selaginella* (5, 16), the root is monarch. In small roots the vascular tissue is poorly developed, the xylem consisting of a small group of from two to five tracheides with the phloem in contact with the metaxylem. In the largest roots examined as many as twelve tracheides were observed, most of them of small size. These small tracheides are sometimes arranged in two groups separated by the larger tracheides. A single layer of pericycle cells appears to be present which may be interrupted by one or more of the tracheides abutting directly on the endodermis.

The stem of *S. pumila* is typically four-sided, with the leaves inserted along the sides (figs. 17, 18). The cells of the epidermal layer are covered by a cuticle and, in young material, the walls are either uniformly lignified or the lignification is confined to the surface walls. In old stems the lignification may extend through the outer cortex, resulting in the formation of a distinct hypodermis. Chlorophyll is specially abundant in the thin-walled cells of the inner cortical layers. Intercellular spaces are present between the cells. The trabeculae which bridge the air space between the inner cortex and pericycle are of a simple type, each consisting of a much elongated endodermal cell showing the usual cuticular band (figs. 17, 18). The single stele is placed somewhat obliquely in the middle of the air space. The one-layered pericycle is usually separated from the xylem by one or more layers of thin-walled phloem cells. Occasionally a xylem tracheide is found to abut directly upon the endodermis. The stele is usually somewhat elliptical in form, with two protoxylem groups.

Stomata are confined to the margin (fig. 19, *a*) and the aligular surface of the leaf. They occur along the vein, often extending beyond its termination, and may appear also on the two wings. With the exception of the

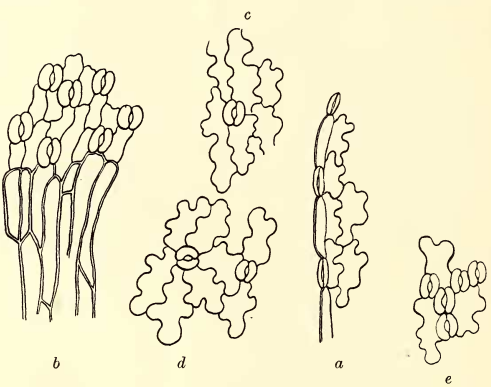


Fig. 19.

cotyledons, a conspicuous leaf-base is present below the insertion of the ligule, and here a definite group of stomata is always found (fig. 19, *b*). Up to twenty stomata have been counted in this region.

The guard cells are placed parallel to the leaf-margin (fig. 19, *c*). Only one instance of a transverse position was noted (fig. 19, *d*). As many as seven epidermal cells may abut upon a single stoma. The number of stomata present may vary within wide limits. When very numerous, adjacent stomata such as those shown in fig. 19, *e*, may occur.

As mentioned above, the leaf-base, except in the cotyledons, is well developed. It contains a mass of aerenchyma roofed over by an epidermis which is perforated by numerous stomata (figs. 19, *b*, 20, 21). Sykes and Stiles (15) describe and figure a similar air cavity in the projecting base of the sporophyll of certain species of *Selaginella*, and compare it with the mucilage cavity of *Lycopodium* and the parichnos of fossil genera. It is also somewhat suggestive of the aerenchyma in the leaf-base of *Miadesmia* (11). This feature does not appear to have been noted before in the vegetative leaf.

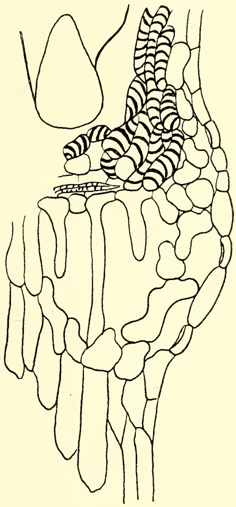


FIG. 20.

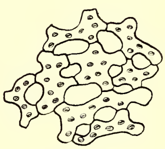


FIG. 21.

The epidermal cells of both surfaces are usually elongated, with sinuous lateral walls (fig. 19). The mesophyll of the leaf-blade shows no differentiation into palisade and spongy parenchyma (fig. 22). It extends right to the leaf-margin.

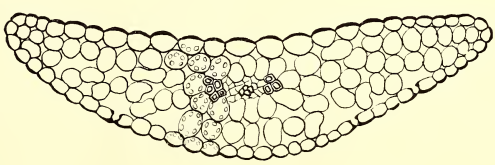


FIG. 22.

The vascular bundle in the cotyledons and lower leaves of the axis is simple, and consists of from four to five rows of delicate spiral and annular tracheides. It does not extend to the apex of the leaf, and, before dying out, it expands slightly owing to the development of several short, flanking tracheides. The next leaves in order of development are found to possess a more complex vascular tissue. The protoxylem of the vein is accompanied by two more or less interrupted groups of spiral and reticulate transfusion *

Fig. 23.

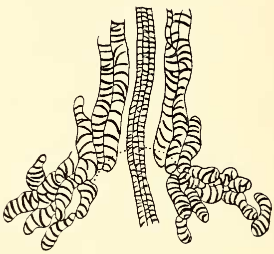


Fig. 24.

tracheides, which may appear at any point between base and apex. All the upper leaves of the plant, including the sporophylls, show two well-developed bands of transfusion tracheides to right and left of the protoxylem (figs. 22, 23, 24). These bands of tracheides do not accompany the leaf-trace into the stem. There is evidently a connection between the amount of transfusion tissue and the number of stomata on the leaf-blade. The only other

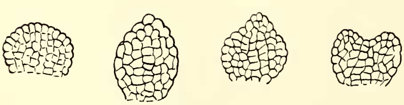


Fig. 25.

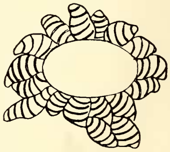


Fig. 26.

species of *Selaginella* in which a similar triple mid-rib has been noted is *S. laevigata*, Bak., var. *Lyallii*, Spr. (5). Bruchmann in 1909 published an account of the vegetative organs of this species (2), but I have not had the opportunity of consulting his paper, nor yet of obtaining material of the species for comparison with *S. pumila*.

The shape of the ligule was found to vary considerably, as shown in

* The use of this term implies no expression of opinion as to the phylogeny of the tissue in question.

fig. 25. The base is surrounded by a well-developed group of reticulate tracheides which is usually continuous with the transfusion elements already described (figs. 24, 26).

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EXPLANATION OF FIGURES.

Fig. 1. Variations in leaf form ; from one plant.

Fig. 2. Abnormal leaf forms.

Fig. 3. Development of first roots at base of hypocotyl of sporeling.

Fig. 4. Plant with unbranched stem and three roots at base of hypocotyl.

Fig. 5, *a–d*. Development of first secondary axis with its root, midway between bases of cotyledons.

Fig. 6. Plant with five secondary axes developed at base. *a*. Hypocotyl shown. *b*. Reverse of fig. *a*.

Fig. 7, *b*. Group of secondary axes removed from primary axis *a*.

Fig. 8. Part of radially symmetric stem with four leaf rows.

Fig. 9. Cotyledons and succeeding leaf-pair cleared in caustic potash.

Fig. 10. Part of stem with three leaf-pairs, one whorl of three leaves, and two alternate leaves.

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* I have had no opportunity of consulting papers (1) to (3).

Fig. 11. Part of stem of unequally illuminated plant showing approach to dorsiventral condition.

Fig. 12. Unequally illuminated plant with two prostrate secondary axes showing dorsiventrality and anisophylly.

Fig. 13. Secondary axis of 12, on a larger scale, showing difference in size of dorsal and ventral leaves.

Fig. 14. Transverse section of young root showing endophytic fungus and cortical cavity.

Fig. 15. Transverse section of old root.

Fig. 16. Transverse section through aerial part of young root of secondary axis.

Fig. 17. Part of transverse section of young stem.

Fig. 18. Section of older stem with base of leaf and ligule.

Fig. 19. *a.* Part of leaf-margin with stomata. *b.* Part of epidermis of leaf-base with stomata abutting upon thickened epidermis of stem destitute of stomata. *c.* Stoma with neighbouring epidermal cells elongated in direction of leaf-margin. *d.* Normally placed stoma and stoma with guard cells transverse to long axis of leaf.

Fig. 20. Vertical section through leaf-base showing aerenchyma, stomata, and tracheides at base of ligule. The leaf-trace is cut obliquely.

Fig. 21. Horizontal section through superficial aerenchyma of leaf-base.

Fig. 22. Transverse section across leaf-blade.

Fig. 23. Outline of leaf showing triple vein, position of ligule, and of stomatal area of leaf-base.

Fig. 24. Part of leaf cleared in caustic potash showing the protoxylem and two parallel bands of transfusion tracheides continuous with reticulate tracheides at base of ligule.

Fig. 25. Variations in shape of ligule. The glossopodial cells are not shown.

Fig. 26. Transverse section through base of ligule showing tracheal sheath.